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# **Age estimation of pouch young and growth of the burrowing bettong, *Bettongia lesueur*, (Marsupialia: Potoroidae) on Heirisson Prong, Shark Bay, Western Australia**

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## **Abstract**

Measurements of hind foot length, weight, head length and tail length were collected from pouch young, young at foot, sub-adults and adults of a reintroduced population of the vulnerable burrowing bettong, *Bettongia lesueur*, on Heirisson Prong, Shark Bay, Western Australia. A key based on qualitative characteristics was used to age individuals and a Richards growth function was fitted to plots of hind foot length versus age. The patterns of growth and morphological characteristics were similar for males and females. Both sexes exhibited a growth pattern typical of a medium-sized macropod with an initial slow phase of growth followed by a rapid phase that slowed as adult size was reached. The growth curves are suitable for broad estimates of the age of wild-caught animals from pouch young to early adulthood.

Keywords: age estimation, bettong, growth, Richards growth curve

The burrowing bettong, *Bettongia lesueur*, is a medium-sized rat-kangaroo native to the arid and semi-arid regions of Australia. Its geographic range contracted dramatically after European settlement, with the only surviving populations on islands off the Western Australian coast (Short and Turner 1993; Burbidge 1998). It is listed as vulnerable under both the Western Australian *Wildlife Conservation Act 1950* and the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999*. In 1992 burrowing bettongs from Dorre Island were reintroduced to Heirisson Prong, Shark Bay, Western Australia where a 12 km<sup>2</sup> section of the long, narrow peninsula was isolated with a barrier fence and foxes, *Vulpes vulpes*, and feral cats, *Felis catus*, controlled in the protected reintroduction area (Short and Turner 2000).

Bettongs were trapped at three-month intervals on Heirisson Prong from 1992 to 1999 (Short and Turner 1999, 2000). Morphometric variables were taken from independent bettongs and furred young ejected from their mothers' pouches during capture. We used these data, together with measurements of pouch young collected during four sampling periods in 2000, to provide the first description of the growth of this species in the wild and to derive growth curves for estimating the age of wild-caught bettongs. The data provide a field-based comparison to the data on the growth of captive animals described by Tyndale-Biscoe (1968) and give quantitative guidelines for placing young animals in age classes.

## **Materials and Methods**

### **Study site**

A site map of Heirisson Prong and detailed descriptions of the topography, vegetation and the reintroduction program were given by Short and Turner (2000).

### **Trapping and measurements**

Bettongs were caught at three monthly intervals on Heirisson Prong for over seven years prior to the start of this study (2000). Retrapping individuals was opportunistic, so while there were often repeated measurements on the same animal, the growth of particular individuals was not specifically followed. Animals were caught in wire-mesh cage traps measuring 550 mm x 200 mm x 200 mm, and baited with a mixture of rolled oats, peanut butter and sardines (Short and Turner 2000). Traps were placed at 100 m intervals along the track system of Heirisson Prong and opened for two or three nights in succession. Animals caught were placed into calico bags for handling and measurement.

Independent bettongs caught for the first time and furred pouch young were individually marked using Passive Implant Transponders (PIT; Trovan ®). The gender, PIT identification, reproductive status, location and date were recorded for each capture, and

measurements of the hind foot length, weight, head length and tail length were taken. Hind foot length measurements were taken from the right foot of adults, from the heel to the end of the fourth digit (longest toe), and excluding the nail. Head length was measured from the base of the skull to the tip of the nose. Tail length was measured from the base of the tail, where it joins the body, along the underside to the tip, and excluding any fur protruding from the end. Lengths were measured with vernier calipers to the nearest 0.1 mm, except tail length which was measured using a flexible tape to the nearest millimetre. Weight measurements were obtained with spring balances to the nearest 10g for adults and to the nearest 5g for large pouch young.

An estimate of measurement error was obtained using the hind foot measurements of pouch young that were measured more than once per monitoring period. The majority of measurements of pouch young were obtained by one of the authors (CF) and therefore interobserver error was not estimated.

Measurements of young in the pouch were made during four monitoring periods in 2000. Hind foot length was the only measurement regularly taken from young in the pouch. More comprehensive measurements were obtained only from young ejected from their mothers' pouch and from independent bettongs.

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In the event of a young being ejected from the pouch, efforts were made to reunite the young with its mother. Unfurred young were reinserted into the pouch and the pouch opening closed with tape. Young that were furred and considered too large for reinserting into the pouch were placed down a burrow with their mother and all openings to the warren blocked with leafy vegetation.

Fourteen female bettongs were fitted with radio-collars in 2000 to enable greater continuity of measurement of their young. During February, March, May and July 2000, when possible, each female was tracked to a warren and traps were set around the warren. This procedure increased the likelihood of recapture as trapping along the track system did not guarantee every female was trapped during every monitoring period.

### **Age estimation of pouch young**

It was assumed that the sequence of pouch young developmental stages of bettongs on Heirisson Prong would be equivalent to those described by Tyndale-Biscoe (1968), even if growth rates varied. Pouch young assessed on Heirisson Prong were placed in an age interval using qualitative observations according to a key developed using the detailed descriptions of developmental stages provided in Tyndale-Biscoe (1968) (Fig. 1).

Age estimates of pouch young were refined further by considering multiple age estimates of individual pouch young on consecutive field trips. Age intervals were narrowed to ensure the number of days between captures fitted the time interval between the two age estimates. For example, if a pouch young aged 22-55 days at first capture was then captured 50 days later and aged 78-88 days, the first age interval could then be narrowed to 28-38 days (78-88 days minus 50 days). The mid point of age intervals was then taken as the age of the pouch young at the time of measurement. These data were then used to construct growth curves.

### **Fitting growth curves**

Growth curves were developed from measurement of 23 individuals first tagged in the pouch that had subsequent captures, including measurements beyond the age of sexual maturity and attainment of adult size. These data were supplemented by measurements from a further 189 pouch young observed in the pouch. All young were aged using the key shown in Fig. 1. Hind foot measurements were used for developing growth curves because this measurement is highly replicable, requires the least handling and causes the least distress to young animals. In particular, this measurement can be made while the young is attached to the teat in the pouch.

The type of growth curve used and the analysis of the results depends on the type of growth data collected (Brisbin *et al.* 1987). Most macropod growth studies have used longitudinal data sets collected by following the growth of captive, known-age

individuals. Data are usually obtained for the most rapid period of growth (pouch life) and often do not extend to adult size. Simpler linear and exponential functions as well as quartic polynomials fit these data best (e.g. Taylor and Rose 1987; Rose 1989; Delaney and De'ath 1990; Johnson and Delean 1999, 2001, 2002). This study utilised a mixed data set extending from birth to adulthood where some individuals were measured only once whilst others were measured several times. For these types of data it is possible to fit sigmoidal curves such as Richards, Gompertz and von Bertalanffy. Several alternatives for choosing a sigmoidal growth curve were explored, including choosing growth curves based on the smallest error sum of squares (i.e. maximising  $R^2$ ). Using this criterion the differences between the fit of Richards, Gompertz and von Bertalanffy growth functions for our data were considered negligible.

Richards growth function was chosen for this study because it allowed the inflection point to occur anywhere in the curve, produced high  $R^2$  values, and allowed calculation of biologically meaningful parameters. The form of Richards growth function used was:

$$Y = b_1 / (1 + b_3 e^{-b_2 x})^{1/b_4}$$

where  $Y$  = body measurement at age  $x$ ,  $x$  = age of the organism at the time of measurement,  $b_1$  = the asymptotic size after growth is completed,  $b_2$  = a

growth parameter controlling the rate of growth,  $b_3$  = a parameter used to calculate the inflection point of the curve, and  $b_4$  = a shape parameter controlling the shape of the curve.



Useful summary statistics can be calculated from these parameters. Bradley et al. (1984) recommend using asymptotic size ( $b_1$ ), weighted mean growth rate ( $R$ ), proportion of asymptotic size reached at inflection ( $P$ ) and the time to pass from ten to 90 percent of asymptotic size ( $G$ ) as summary statistics for describing the growth pattern of an organism. The latter is also an indication of the period of time that measurements provide good resolution for estimating age (i.e. the steepest part of the curve). The statistics may be defined as follows where  $b_1$  = raw parameter from the curve,  $R = b_2/M$  (where  $M = b_4 + 1$ ),  $P = M^{1/(1-M)}$ , and  $G = \ln((1-0.1^{1-M})/(1-0.9^{1-M}))/b_2$ . The time to reach inflection may be defined as  $I = (\ln b_3 - \ln b_4)/b_2$ .

Growth curves were fitted to the data using the nonlinear regression (NLR) and constrained non-linear regression module (CLNR) of the SPSS statistical package Version 12 (SPSS Inc. 2003). Satisfactory results were achieved when:

- (1) the  $R^2$  values indicated a good fit;
- (2) residuals were approximately normally distributed;
- (3) visual inspection of the curve through the data was considered acceptable.

Confidence limits (95%) for age were obtained from the corresponding 95% confidence limits of the predicted lengths (Wood *et al.* 1981).

To determine if separate growth curves were required for males and females, the average body measurements of male and female bettongs weighing 880g were compared to check for sexual dimorphism in adults. Average measurements of bettongs weighing 880g were used for direct comparison to the data reported in Short and Turner (1999) who noted

880g as the lowest weight at which a female was confirmed reproductive. Even if there is no adult sexual dimorphism, males and females may still reach adulthood at different rates. To check for this, growth curves for males and females were determined separately.

The Akaike Information Criterion (AIC) was also used to inform selection of a separate curve for each sex versus a unified curve (Burnham and Anderson 1998). The AIC can only be used to compare nested models, i.e. when one model forms part of a subset, with a reduced number of parameters, of the model it is being compared with. In the case of comparisons between two models the reduced model (i.e. the model with fewer parameters) is nested within the saturated model, and the difference between the values of the AIC ( $\Delta AIC$ ) is used as a criterion for model selection. Following Burnham and Anderson (1998) we have accepted a  $\Delta AIC$  of  $> 7$  as strong evidence of a real difference between models and in these cases have retained the saturated rather than the reduced model.

A final check of the data was made to assess the effect of repeated measures and maternity because some individuals were measured many times whilst others only a few and some mothers may have been more successful at raising young than others. The data were sub-sampled by randomly selecting a single day's measurements from a single pouch young of each mother.

A growth curve was fitted also to the raw unpublished data of hind foot length measurements of captive pouch young that formed the basis of Tyndale-Biscoe (1968).

Data from two males and two females were insufficient for the sexes to be treated separately so the data were combined and the growth curve compared to that derived for Heirisson Prong animals. This comparison was complicated because Heirisson Prong animals were initially placed in an age interval based on the physical characteristics of developmental stages observed from the pouch young of the captive population. Despite this, it was considered useful to know if the refinements on age of Heirisson Prong animals arising from multiple measurements ultimately contributed to a different growth curve for the Heirisson Prong population, compared with the captive animals.

## **Results**

### **Trapping and measurements**

In total, 579 bettongs (282 males and 297 females) were marked individually between 1992 and February 2001 (Short and Turner 2000 and J. Short unpublished data). Each animal was measured on one or more occasions and the data were used to calculate the average adult size. A subset of 199 females was monitored more closely in 2000 to enable examination of pouch young.

Measurements of hind foot length, weight, head length and tail length for adult males and females collated from the trapping records are shown in Table 1. Largest sample sizes were available for hind foot length and weight measurements. Average adult

measurements of two island populations of burrowing bettongs (Short and Turner 1999) are shown alongside those of Heirisson Prong animals in Table 1.

An estimate of measurement error was obtained from seven pouch young that had multiple hind foot measurements during a single monitoring period. The average range in hind foot measurements for these seven pouch young was 1.3 mm. This is an upper estimate of measurement error because the multiple measurements used in the estimate were taken over a period of between one and four days and therefore some of the difference must be attributed to growth because growth rate is most rapid during pouch life. The small sample size of multiple measurements and the complication of growth between measurements precluded a more comprehensive assessment of measurement error.

### **Age estimation of pouch young**

The pouch young of 199 mothers were observed with 110 of those mothers captured on more than one occasion. This resulted in most pouch young having multiple age estimates made during consecutive monitoring periods whilst others were measured on non-consecutive monitoring periods. Twelve pouch young were observed more than once per monitoring period. Some mothers contributed no pouch young whilst others contributed more than one.

During this study, 343 hind foot length measurements were obtained from 189 pouch young (93 males, 76 females and 20 unsexed). Twenty three individuals were PIT tagged in the pouch as large furred pouch young and subsequently recaptured.

### **Fitting growth curves**

A single measurement from a single pouch young from each mother was randomly selected from the data to remove possible effects of repeated measures and maternity. This decreased the data set by 56%, and hence reduced the power of the data to test comparisons. In addition, because fewer mothers were represented in the observations of older progeny, the reduction fell most heavily on later measurements. We estimated growth parameters from the full data set because the sub-sampled data had relatively few observations in the later stages of growth since these observations tended to be generated as part of repeated measurement sets on a limited number of individuals. As a consequence, the determination of the asymptote was much less precise in the reduced data set.

Sexual dimorphism in adults was checked using trapping data collected since 1992 of bettong weighing 880 g. As a consequence of this large data set (Table 1), adult male and female burrowing bettongs weighing 880 g were found to be significantly different for hind foot length ( $z = -7.61$ ,  $p < 0.001$ ) (females 100.1 mm, males 102.2 mm), a difference of only 2.1 mm or about 2% of male hind foot length. In the field, this small difference is likely to be indistinguishable from measuring error. However, the  $\Delta AIC$  criterion also

indicated that fitting separate hind foot growth curves for the sexes was appropriate. Separate growth curves were therefore fitted for males and females and plotted on the same graph (Fig. 2). This graph also allows comparison of the shapes of the curves for males and females.

The growth curves for males and females are very similar (Fig. 2). This similarity is also evident in the growth curve parameters and summary statistics presented in Table 2. On the basis of this similarity and the trivial sexual dimorphism of the adults, data from males and females were also combined. The curve derived from the combined data for Heirisson Prong was used to compare to the curve derived from captive population data (Fig. 3).

The pouch young from the captive Heirisson Prong populations exhibited the same changes in growth rate as they developed; however, the captive population took longer to pass the first phase (Fig. 3). The Heirisson Prong pouch young reach the asymptote of the curve earlier (determined by visual inspection) as well as the inflection point (I) of the curve (64 days rather than 77 days; Table 2).

By visual inspection, the growth curve fitted for hind foot length of the Heirisson Prong population over-estimates the age of pouch young less than two weeks old (Fig. 3). This was not considered a problem as hind foot length cannot be measured accurately for the first 12 days (Tyndale-Biscoe 1968) as the features of the hind foot are not fully

developed. At this young age the key may be used to estimate age from physical characteristics.

Predicted hind foot lengths, their 95% confidence limits and the corresponding limits of age are listed in Table 3. This table may be used to estimate the age of young in the pouch.

## **Discussion**

### **Methodological issues in estimating the age of pouch young**

The key developed during this study from information on pouch young development provided by Tyndale-Biscoe (1968) was useful in estimating an initial age class for pouch young on first capture and this age was refined with multiple captures over time.

However, there were difficulties in interpreting the key but these were resolved through experience. Unfused ears may be mistaken for fused ears and female pouch young may be misidentified as too young to sex. Other issues were resolved through multiple captures.

These included age estimation difficulties associated with observing characteristics such as the ability of the pouch young to right itself out of the pouch when the mother had not ejected it from the pouch, and the difficulty in observing the ability of the pouch young to squeak. It is also worthwhile to note that later age intervals in the key overlap, requiring consideration of all characteristics of the pouch young before assigning an age.

There is a large gap in the key from day 22 to 55. The characteristics of this age interval were not observed to develop in a more precise way within this age interval by Tyndale-Biscoe (1968) and so accuracy relied on previous or subsequent captures to refine the age estimate. All these methodological issues in estimating the age using the key were resolved through experience and multiple captures of individuals. It is therefore recommended that the key be used on at least two separate occasions for each pouch young, to improve the accuracy of the age estimate.

### **Interpretation of growth curves**

The only previous study of growth in the burrowing bettong was by Tyndale-Biscoe (1968), who studied the growth of captive bettongs as part of an investigation into the reproduction and post-natal development of the species. Tyndale-Biscoe (1968) derived growth curves from four pouch young monitored closely from birth to permanent pouch emergence and described the development of 42 pouch young, only four of which reached permanent pouch emergence. New growth curves based on the Heirisson Prong population are of interest because:

1. Heirisson Prong animals were sourced from Dorre Island whereas the population studied by Tyndale-Biscoe (1968) was sourced from Bernier Island. Short and Turner (1999) noted significant, albeit small, morphological differences between adult burrowing bettongs on Bernier and Dorre Island.
2. The animals on Heirisson Prong are a free-ranging wild population. Numerous studies concluded there are significant differences between the growth of captive



and wild populations (e.g. Inns 1982; Taylor and rose 1987, Delaney and De'ath 1990).

3. Tyndale-Biscoe (1968) only had access to a very small sample size of four individuals suitable for developing growth curves, and these may have been unrepresentative of the species.

The shape of the captive and Heirisson Prong growth curves for hind foot are similar as indicated by the summary statistics M, R, P and G. However the time to reach inflection (I) is longer for the captive population (78 vs 64 days; Table 2) which corresponds to a slower first phase of development in the captive population.

The growth curves for the burrowing bettong may be divided into three phases: an initial phase of slow growth in the first three weeks, followed by a rapid growth phase that slows after 12 weeks until adult size is reached. This is a typical pattern of growth for small macropods with an initial phase of slow growth followed by a rapid phase that slows as adult size is reached. For example, Maynes (1976) describes two phases of growth in the parma wallaby, *Macropus parma*. The first phase of slower growth is thought by Maynes (1976) to be a continuation of embryonic organogenesis and differentiation. The second phase of more rapid growth, as partly indicated by the 22-55 day age gap in our key, is a period of maturation and growth in size of the organs developed during gestation and the first phase of growth. A final change in growth rate occurs when hair appears, eyes open and the young first leave the pouch. It is at this time that the thyroid gland becomes active and the young develop the ability to thermoregulate (Gemmell and Rose 1989; Gemmell and Hendrikz 1993). Thermoregulation coincides

with the appearance of fur in Tasmanian bettongs, *Bettongia gaimardi* (Rose *et al.* 1998) and in quokkas, *Setonix brachyurus* (Loh and Shield 1977). Janssens and Rogers (1989) suggest the development of the ability to thermoregulate plays an important role in pouch vacation in the tammar wallaby, *Macropus eugenii*, and other macropods. Once young leave the pouch, growth rate slows as energy is diverted into thermoregulation, locomotion and adjusting to a diet that consists of more than just milk (Maynes 1976; Rose and McCartney 1982). Burrowing bettongs in captivity have been recorded leaving the pouch at around 115 days and this coincides with a rapid slowing of growth rate (Tyndale-Biscoe 1968).

Animal husbandry problems discussed by Tyndale-Biscoe (1968) as possible reasons for the low pouch young survival rate observed for the captive population (11.1% vs 77.8% this study, unpublished data), may help to explain the comparatively slower first phase of growth. These reasons included the failure of the mother to produce enough milk with adequate nutrients, and possible nutritional or endocrine problems arising from the artificial diet. It is possible the artificial diet did not provide all the nutrients and variety found in the natural diet on Heirisson Prong (Tyndale-Biscoe 1968).

Another possible explanation is that the development of the captive pouch young was delayed as a result of disturbance in early pouch life. Between about a week and almost two months of age the young is permanently attached to the teat and can only voluntarily detach from the teat after this period. Removing young from the pouch during this period for weighing and measurement, as in the study by Tyndale-Biscoe (1968), may result in the young not being able to reattach to the teat quickly and therefore delaying continued

suckling. Nearly 70% of pouch young deaths observed by Tyndale-Biscoe (1968) were less than 20 days old, which corresponds to the early part of the period where young cannot voluntarily detach from the teat. In the Heirisson Prong study no pouch young were detached from the teat or removed from the pouch unless the mother had ejected them.

There are errors associated with both the hind foot measurement and the age estimate for each data point in this study that result in large confidence intervals. Other studies with smaller confidence limits have used captive populations where the birth date of pouch young is known and measurement was therefore the only source of error (e.g. Poole et al. 1982; Hendrikz and Johnson 1999). To reduce measurement error in future studies, or at least quantify it, it is recommended that researchers follow the advice of Blackwell et al. (2006) and take at least two replicate measurements per morphometric variable being considered.

Growth of pouch young is known to be correlated with maternal weight, with pouch young of heavier mothers developing faster than those from lighter mothers (Green et al. 1988). Maternal weight varied quite considerably in the free-ranging population and this may partly explain the variability in measurements of pouch young at the same age as well as the high residual sum of squares for the fit of the curves.

We provide a method to estimate the age of pouch young of the burrowing bettong from both physical characteristics and hind foot measurement. We chose hind foot length as

our preferred body measurement because of the minimal impact on the young, but we cannot exclude the possibility that age estimates could be improved by using other measurements or a combination of measurements. Age estimates of young derived from the developmental key of physical attributes can be further refined if individuals are captured and assessed for an age estimate more than once.

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## References

- Blackwell GL, Bassett SM and Dickman CR, 2006. Measurement error associated with external measurements commonly used in small-mammal studies. *Journal of Mammalogy* 87: 216-223.
- Bradley A, Landry R and Collins A, 1984. The use of Jackknife confidence intervals with the Richards curve for describing avian growth patterns. *Bulletin of the Southern California Academy of Science* 83, 133-147.
- Brisbin IL, Collins CT, White GC and McCallum DA, 1987. A new paradigm for the analysis and interpretation of growth data: The shape of things to come. *Auk* 104, 552-554.
- Burbidge AA, 1998. Burrowing bettong. Pp. 289-291 in *The Mammals of Australia* ed by R Strahan. Reed Books: Sydney.
- Burnham KP and Anderson DR, 1998. *Model Selection and Inference – A Practical Information Theoretical Approach*. Springer Verlag: New York.
- Delaney R and De'ath G, 1990. Age estimation and growth rates of captive and wild pouch young of *Petrogale assimilis*. *Australian Wildlife Research* 17, 491-499.
- Gemmell RT and Hendrikz J, 1993. Growth rates of the bandicoot *Isodon macrourus* and the brushtail possum *Trichosurus vulpecula*. *Australian Journal of Zoology* 41, 141-149.
- Gemmell RT and Rose RW, 1989. Organ development in some newborn marsupials with particular reference to the rat-kangaroo. Pp. 349-354 in *Kangaroos, Wallabies and Rat-Kangaroos* ed by G Grigg, P Jarman and I Hume. Surrey Beatty and Sons: Chipping Norton, NSW.
- Green B, Merchant J and Newgrain K, 1988. Milk consumption and energetics of growth in pouch young of the tammar wallaby, *Macropus eugenii*. *Australian Journal of Zoology* 36, 217-227.
- Hendrikz JK and Johnson PM, 1999. Development of the bridled nailtail wallaby, *Onychogalea fraenata*, and age estimation of the pouch young. *Wildlife Research* 26, 239-249.
- Inns RW, 1982. Age determination in the Kangaroo Island Wallaby, *Macropus eugenii* (Desmarest). *Australian Wildlife Research* 9, 213-220.
- Janssens P and Rogers A, 1989. Metabolic changes during pouch vacation and weaning in macropodoids. Pp 367-376 in *Kangaroos, Wallabies and Rat-Kangaroos* ed by G Grigg, P Jarman and I Hume. Surrey Beatty and Sons: Chipping Norton, NSW.
- Johnson PM and Delean JSC, 1999. Reproduction in the Proserpine rock-wallaby, *Petrogale persephone* Maynes (Marsupialia, Macropodidae), in captivity, with age estimation and development of pouch young. *Wildlife Research* 26, 631-639.
- Johnson PM and Delean S, 2001. Reproduction in the northern bettong, *Bettongia tropica* Wakefield (Marsupialia, Potoroidae), in captivity with age estimation and development of pouch young. *Wildlife Research* 28, 79-85.
- Johnson P and Delean S, 2002. Reproduction of the purple-necked rock-wallaby, *Petrogale purpureicollis* Le Souef (Marsupialia, Macropodidae), in captivity, with age estimation and development of pouch young. *Wildlife Research* 29, 463-468.
- Loh T and Shield J, 1977. Temperature regulation and oxygen consumption in the developing macropod marsupial *Setonix brachyurus*. *Journal of Physiology* 269, 677-686.

- Maynes GM, 1976. Growth of the parma wallaby, *Macropus parma* Waterhouse. *Australian Journal of Zoology* 24, 217-236.
- Poole WE, Carpenter SM and Wood JT, 1982. Growth of grey kangaroos and the reliability of age determination from body measurements I. The eastern grey kangaroo, *Macropus giganteus*. *Australian Wildlife Research* 9, 9-20.
- Rose RW, 1989. Age estimation in the Tasmanian bettong (*Bettongia gaimardi*) (Marsupialia: Potoroidae). *Australian Wildlife Research* 16, 251-261.
- Rose RW, Kuswanti N and Coloquhoun E, 1998. Development of endothermy in a Tasmanian marsupial, *Bettongia gaimardi*, and its response to cold and noradrenaline. *Journal of Comparative Physiology B: Biochemical, Systematic and Environmental Physiology* 168, 359-363.
- Rose RW and McCartney DJ, 1982. Growth of the red-bellied pademelon, *Thylogale billardieri*, and age estimation of pouch young. *Australian Wildlife Research* 9, 33-38.
- Short J and Turner B, 1993. The distribution and abundance of the burrowing bettong, (Marsupialia: Macropodidae). *Wildlife Research* 20, 525-534.
- Short J and Turner B, 1999. Ecology of burrowing bettongs, *Bettongia lesueur* Marsupialia: Potoroidae), on Dorre and Bernier Island, Western Australia. *Wildlife Research* 26, 651-669.
- Short J and Turner B, 2000. Reintroduction of the burrowing bettong *Bettongia lesueur* (Marsupialia: Potoroidae) to mainland Australia. *Biological Conservation* 96, 185-196.
- SPSS Inc, 2003. Statistical Package for the Social Sciences V12. (SPSS Inc., Chicago.)
- Taylor RJ and Rose RW, 1987. Comparison of growth of pouch young of the Tasmanian bettong, *Bettongia gaimardi*, in captivity and in the wild. *Australian Wildlife Research* 14, 257-262.
- Tyndale-Biscoe CH, 1968. Reproduction and post-natal development in the marsupial *Bettongia lesueur* (Quoy & Gaimard). *Australian Journal of Zoology* 16, 577-602.
- Wood JT, Carpenter SM and Poole WE, 1981. Confidence intervals for ages of marsupials determined by body measurements. *Australian Wildlife Research* 8, 269-274.

Fig. 1. Ageing key for pouch young of the burrowing bettong, developed from information provided in Tyndale-Biscoe (1968).

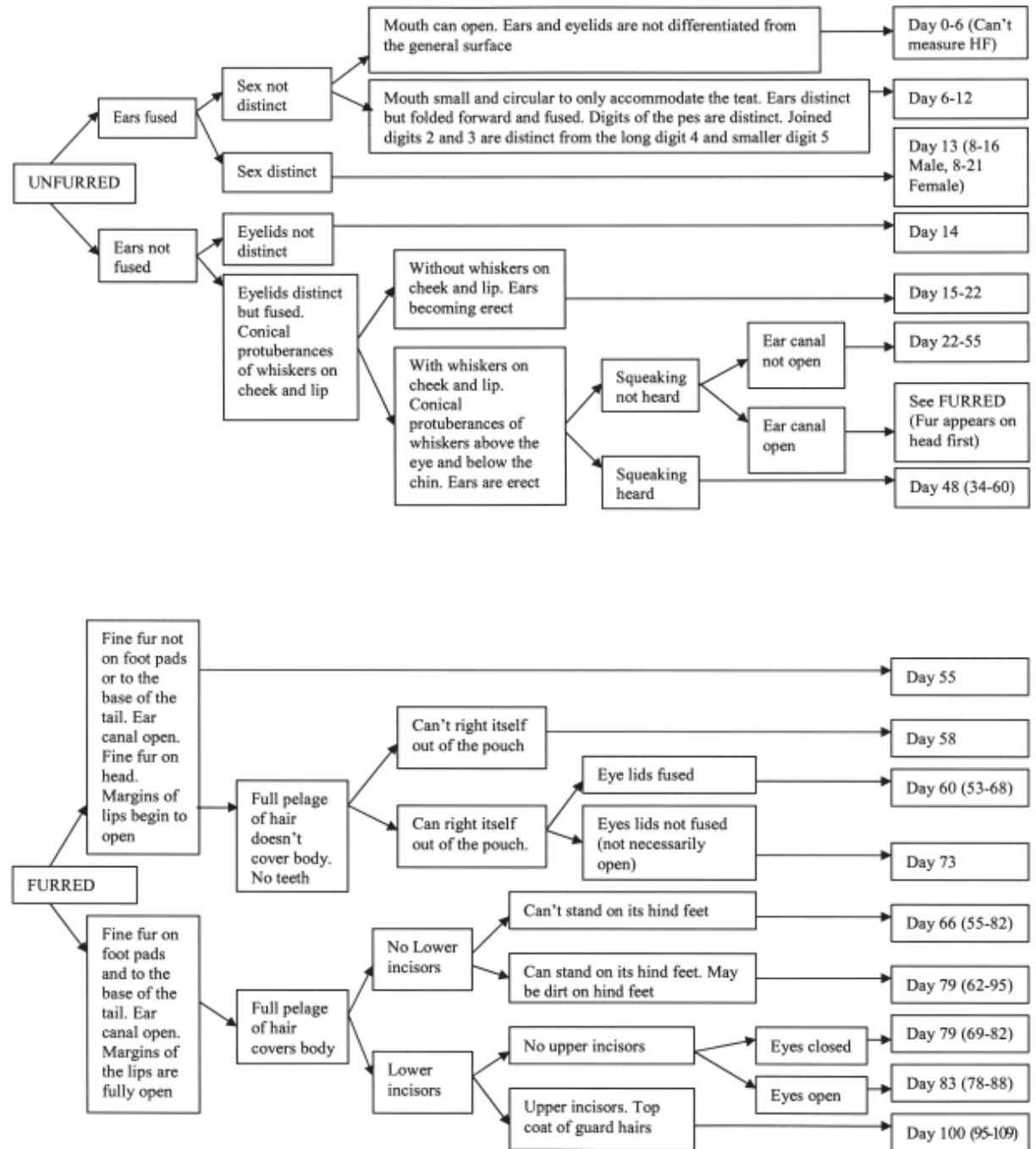
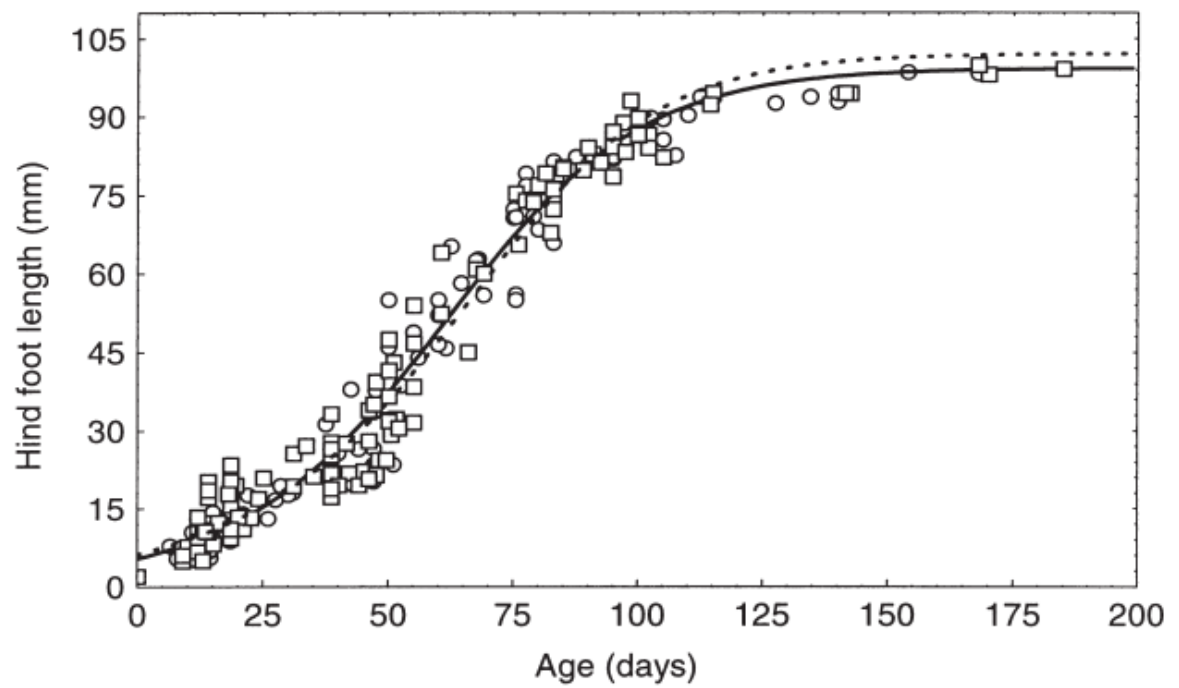


Fig. 2. Hind foot growth curves for male (----,  $\square$ ) and female (\_\_\_\_,  $\circ$ ) burrowing bettongs from Heirisson Prong. Note: data used to fit the curve extended beyond the 200 days shown, to 1065 days.





*Fig. 3.* Comparison of hind foot length growth curves for burrowing bettongs from Heirisson Prong (\_\_\_\_, ○) and captive (-----, Δ) populations. Note: data used to fit the curve extends beyond the 200 days shown (i.e. 341 days for the captive population and 1065 days for the Heirisson Prong population).

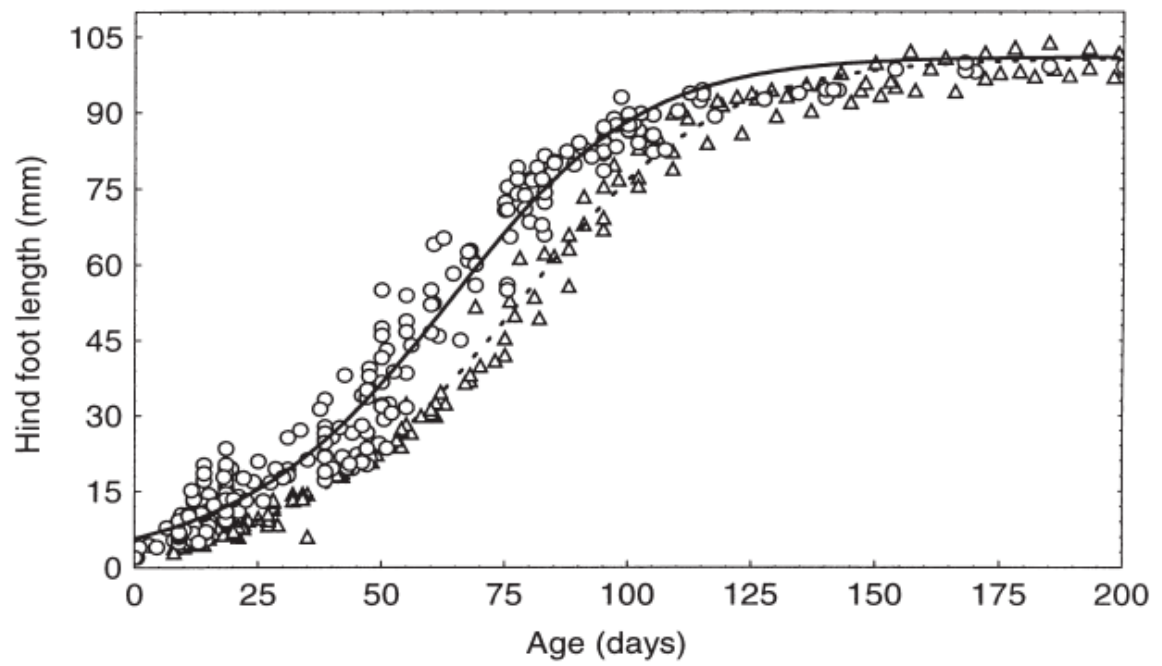


Table 1. Comparison of average adult measurements ( $\pm$  S.E.) for burrowing bettongs weighing 880 g on Heirisson Prong (this study) and Bernier and Dorre Island (Short and Turner 1999).

|                 | Sex    |         | Hind foot<br>length (mm) | Weight<br>(g) | Tail length<br>(mm) | Head length<br>(mm) |
|-----------------|--------|---------|--------------------------|---------------|---------------------|---------------------|
| Heirisson Prong | All    | Average | 101.1 (0.1)              | 1356 (9)      | 300.1 (1.1)         | 77.9 (0.3)          |
|                 |        | n       | 578                      | 579           | 318                 | 351                 |
|                 | Male   | Average | 102.1 (0.2)              | 1359 (6)      | 302.6 (1.6)         | 78.0 (0.4)          |
|                 |        | n       | 281                      | 282           | 154                 | 173                 |
| Bernier Island  | Female | Average | 100.1 (0.2)              | 1354 (12)     | 290.7 (0.5)         | 77.8 (0.4)          |
|                 |        | n       | 297                      | 297           | 164                 | 178                 |
|                 | All    | Average | 100.2 (0.03)             | 1263 (14)     | 279.5 (0.14)        | 73.2 (0.03)         |
|                 |        | n       | 130                      | 130           | 130                 | 129                 |
| Dorre Island    | All    | Average | 98.0 (0.2)               | 1312 (9)      | 286.9 (1.1)         | 74.5 (0.3)          |
|                 |        | n       | 417                      | 421           | 313                 | 320                 |

Table 2. Burrowing bettong growth curve parameters and summary statistics. Standard errors are in brackets. The Akaike differences ( $\Delta AIC$ ) are calculated from the sub-sampled data set and refer to the comparison of the combined sex models with the individual sex models. All other values in the table refer to the full data set.  $b_1$  = Asymptote;  $I$  = the time to reach inflection point;  $M$  = a shape constant controlling the shape of the curve;  $R$  = weighted mean growth rate;  $P$  = proportion of asymptotic size achieved at inflection;  $G$  = time to pass from 10 – 90% of asymptotic size.

| Measurement                              | sex    | $b_1$            | $b_2$          | $b_3$            | $b_4$          | n   | $R^2$ | Residual<br>ss | $\Delta AIC$   | $I$<br>(days) | $M$  | $R$  | $P$  | $G$<br>(days) |
|--|--------|------------------|----------------|------------------|----------------|-----|-------|----------------|----------------|---------------|------|------|------|---------------|
|  | all    | 101.24<br>(0.55) | 0.05<br>(0.00) | 37.23<br>(17.05) | 1.29<br>(0.19) | 320 | 0.98  | 8828.15        | 10.71<br>1.04% | 64.3          | 2.29 | 0.02 | 0.53 | 92.6          |
| Heirsson<br>Prong<br>hind foot<br>length | male   | 102.30<br>(0.67) | 0.06<br>(0.01) | 65.24<br>(44.23) | 1.52<br>(0.29) | 183 | 0.98  | 3580.62        |                | 67.6          | 2.52 | 0.02 | 0.54 | 93.7          |
|  | female | 99.41<br>(0.89)  | 0.05<br>(0.01) | 24.64<br>(15.93) | 1.13<br>(0.26) | 138 | 0.98  | 3580.62        |                | 60.9          | 2.13 | 0.02 | 0.51 | 90.5          |
| Captive<br>hind foot<br>length           | all    | 100.93<br>(0.41) | 0.05<br>(0.00) | 57.80<br>(22.00) | 1.21<br>(0.14) | 200 | 0.99  | 2028.42        | -<br>-         | 77.5          | 2.21 | 0.02 | 0.52 | 94.5          |

Table 3. Age of burrowing bettongs, predicted values of hind foot length with 95% confidence limits, and corresponding limits for age.

| Age<br>(days) | Lower<br>limit | Upper<br>limit | Predicted<br>hind foot<br>length<br>(mm) | Lower<br>95%<br>limit | Upper<br>95%<br>limit |
|---------------|----------------|----------------|--|-----------------------|-----------------------|
| 14            | 0              | 31             | 10                                       | 0                     | 20                    |
| 18            | 0              | 34             | 12                                       | 2                     | 21                    |
| 22            | 0              | 36             | 14                                       | 4                     | 23                    |
| 26            | 2              | 39             | 16                                       | 6                     | 26                    |
| 30            | 11             | 42             | 18                                       | 9                     | 28                    |
| 34            | 18             | 45             | 21                                       | 12                    | 31                    |
| 38            | 24             | 48             | 25                                       | 15                    | 34                    |
| 42            | 30             | 51             | 28                                       | 19                    | 38                    |
| 46            | 35             | 55             | 32                                       | 23                    | 42                    |
| 50            | 40             | 58             | 36                                       | 27                    | 46                    |
| 54            | 45             | 62             | 41                                       | 31                    | 51                    |
| 58            | 50             | 66             | 46                                       | 36                    | 55                    |
| 62            | 54             | 70             | 51                                       | 41                    | 60                    |
| 66            | 58             | 74             | 56                                       | 46                    | 65                    |
| 70            | 62             | 78             | 60                                       | 51                    | 70                    |
| 74            | 66             | 83             | 65                                       | 56                    | 75                    |
| 78            | 70             | 88             | 70                                       | 60                    | 79                    |
| 82            | 73             | 93             | 74                                       | 64                    | 84                    |
| 86            | 76             | 98             | 78                                       | 68                    | 87                    |
| 90            | 80             | 105            | 81                                       | 72                    | 91                    |
| 94            | 83             | 112            | 84                                       | 75                    | 94                    |
| 98            | 86             | 122            | 87                                       | 77                    | 97                    |
| 102           | 88             | 137            | 89                                       | 80                    | 99                    |
| 106           | 91             | 207            | 91                                       | 82                    | 101                   |
| 110           | 93             | -              | 93                                       | 83                    | 103                   |
| 114           | 95             | -              | 95                                       | 85                    | 104                   |
| 118           | 97             | -              | 96                                       | 86                    | 105                   |
| 122           | 98             | -              | 97                                       | 87                    | 106                   |
| 126           | 99             | -              | 98                                       | 88                    | 107                   |
| 130           | 100            | -              | 98                                       | 89                    | 108                   |
| 134           | 101            | -              | 99                                       | 89                    | 108                   |
| 138           | 102            | -              | 99                                       | 90                    | 109                   |
| 142           | 103            | -              | 100                                      | 90                    | 109                   |
| 146           | 104            | -              | 100                                      | 90                    | 109                   |
| 150           | 104            | -              | 100                                      | 90                    | 110                   |
| 154           | 104            | -              | 100                                      | 91                    | 110                   |
| 158           | 105            | -              | 100                                      | 91                    | 110                   |
| 192           | 105            | -              | 101                                      | 91                    | 110                   |